

BIPOLAR VARIATION IN *CLIONE*, A GYMNASOMATOUS PTEROPOD

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ABSTRACT

The gymnosome *Clione* inhabits waters of the Arctic, North Pacific, North Atlantic, South Atlantic and Antarctic Oceans. This study reexamines bipolarity in this genus, utilizing new morphological techniques as well as observations of living animals in all locales. Differences in external anatomy are readily apparent in both larval and adult *Clione* from northern and southern areas, and scanning electron microscopy has revealed differences in the number and size of hooks in animals from different regions. The configuration of the radula differs between specimens from the northern and southern hemispheres, and *Clione* from the Antarctic lacks median radular teeth, in contrast to the well developed, sickle-shaped median teeth present in *Clione* from northern areas. *Clione* acts as a food specialist throughout its range, feeding either on the bipolar thecosome species *Limacina helicina* (Phipps) in cold waters or *L. retroversa* (Fleming) in temperate waters. Differences in maximum adult size of *Clione* can be related to the size of available prey. Although there do not appear to be differences in the feeding behavior of *Clione* from different areas, there are slight differences in swimming and escape behavior, particularly between specimens of *Clione* from northern and southern regions. The results of these anatomical and behavioral observations support the validity of recognizing two species of *Clione*, *C. limacina* (Phipps) in the northern hemisphere and *C. antarctica* (Smith) in the Antarctic and South Atlantic oceans.

The gymnosome now called *Clione limacina* (Phipps) was originally illustrated in a publication by Martens in 1675, from specimens collected in waters off Spitzbergen and Greenland. However, Captain C. J. Phipps is credited with the first taxonomic description, which appeared in his 1774 book entitled *A Voyage Towards the North Pole*. Since these early descriptions, many publications have dealt with this species, the most abundant gymnosome in temperate and cold northern waters. It has been recognized as an important food for baleen whales and certain commercial species of fish (see Lalli and Gilmer, 1989).

Since the late 1700s, a species of *Clione* has also been known to exist in cold waters of the southern hemisphere. Early illustrations and taxonomic history of the northern and southern *Clione* can be found in Rang and Souleyet (1852) under the respective names of *Clio borealis* (Rang and Souleyet) and *C. australis* (Rang and Souleyet). The southern

Clione has been variously considered as a variety, form, or subspecies of *C. limacina* [see van der Spoel (1976) for synonymy], or as a separate species, *C. antarctica*, described by Smith in 1902. The southern *Clione* is less well known than the Arctic/Subarctic species, but preserved specimens were admirably described by Eliot (1907), who pointed out several anatomical differences between *C. antarctica* (Smith) and northern *C. limacina*. Additional anatomical studies of *C. antarctica* have been made by Meisenheimer (1906), Massy (1920, 1932) and Pruvot-Fol (1932), among others.

Clione limacina is found throughout the central Arctic Ocean, and extends in Subarctic waters southward into both the North Atlantic and North Pacific to approximately 30° to 40° North latitude. The southern hemisphere *Clione* is found circumglobally in Subantarctic and Antarctic waters, extending northward to about 40°. Because there are no connecting populations in tropical areas, these gymnosomes have

been considered as one of several examples of bipolarity in plankton (Ekman, 1953).

Our objectives here included direct comparisons of the morphological and behavioral differences between northern and southern populations of *Clione* in order to investigate their taxonomic distinction. We have compared our behavioral observations of several hundred living animals made during the Hudson 70 Expedition to Antarctic waters in 1970 by one of us (CML) and during two visits to Antarctica in 1987 and 1988 by the other of us (RWG), to those of living *Clione* observed in both the North Atlantic and North Pacific over a period of many years. We have also made anatomical and histological comparisons of specimens of *Clione* from several locations, using scanning electron microscopy to investigate detail not noted previously.

METHODS

Specimens of *Clione* were collected by plankton nets or by scuba divers at various locations throughout its range. Behavioral observations were noted *in situ* by divers or in laboratory aquaria. For anatomical studies, specimens representing a range of size categories were narcotized with MS222 (Ethyl m-aminobenzoate) and then preserved in either Bouin's fluid or 4% formaldehyde. Radulae and hooks were dissected from specimens, and extraneous tissue was removed by soaking in a dilute bleach solution. After rinsing in an alcohol series, the buccal structures were mounted on stubs with double stick tape, coated with gold, and examined on either a Cambridge Stereoscan 250 or a Novascan 30 scanning electron microscope. In all, radulae were examined from over 20 specimens collected across the regions under study. Histological sections of 10 μ m thickness were made of four *Clione antarctica* and stained using Cason's modification of Mallory's triple stain (Humason, 1962).

RESULTS

COMPARISON OF EXTERNAL ADULT MORPHOLOGY

Adult specimens of *Clione limacina* from the North Pacific and North Atlantic are anatomically similar (Figs. 1a, b), despite differences in size. *Clione* attains a maximal size of about 30 mm in length in the North Pacific Ocean, whereas adult specimens in arctic and subarctic waters of the North Atlantic Ocean commonly reach a length of 70 to 85 mm (Table 1), the largest size of any gymnosome. The maximal size of *C. limacina* diminishes in more temperate waters of the North Atlantic Ocean; sexually mature specimens are usually less than 25 mm long in waters south of Nova Scotia, Canada, and are less than 12 mm long in the English Channel.

Clione antarctica (Fig. 1c) attain a maximal length of about 42 mm, and it is strikingly different in external appearance from the northern species of *Clione*. The head of *C. antarctica* is elongate compared with that of *C. limacina*, and the demarkation between the head and the remainder of the body is not as clear. The head comprises about one-quarter to one-fifth of the total body length, whereas the head

of *C. limacina* is smaller relative to total body length, constituting less than one-seventh of the total body length of extended, living animals. The anterior tentacles of *C. antarctica* are noticeably smaller than those of the northern hemisphere species, but both species have similarly sized posterior tentacles located in depressions on the dorsal surface of the head.

Clione antarctica adults retain evidence of all three larval ciliary rings that are characteristic of gymnosome polytroch larvae, although the cilia can disappear. The first ring persists as distinct and separate protuberances encircling the mid-section of the head. The second and third rings persist as transparent bands that encircle the mid-trunk and the posterior tip of the body, respectively. In *C. limacina*, the anterior and middle larval rings disappear rapidly and completely during metamorphosis of the polytrochous larva to the juvenile form; the third or posterior band can persist through the juvenile stage, but it is not evident in sexually mature adults, except in English Channel populations. The posterior tip of the body of adult *C. antarctica* is marked by the constriction of the posterior larval ring, followed by an expanded triangular area. This is identical to the form of the posterior tip in young juvenile *C. limacina* but, in adults, the constriction is lost and the posterior end tapers gradually to a point.

Adults of *Clione antarctica* also differ from the northern species in that the viscera extends three-quarters of the way to the posterior tip of the body. In *C. limacina*, the viscera can occupy the entire body of larvae and juveniles but, in adults, the visceral mass does not extend beyond the anterior one-half of the body; the posterior half of the adult body is a fluid-filled cavity.

Body coloration is somewhat variable among individuals but, in both species, the prehensile buccal cones are reddish-orange. The posterior tip is brightly pigmented in some specimens of *Clione limacina*, but it is usually transparent or only faintly colored in *C. antarctica*. The digestive gland of both species is usually yellowish-orange or orange, but is dark brown immediately after feeding. Coloration in general is probably derived at least partly from diet, as starved animals lose the striking red color from the cones. The wings and integument are transparent, but slightly less so in specimens of *C. antarctica* which can exhibit some degree of opacity. Eliot (1907) stated that the integument of preserved specimens of *C. antarctica* contained more "yellow spots" than that of *C. limacina*. This statement apparently refers to oil droplets embedded in the integument, and Eliot's statement is true when comparing adults. However, polytrochous larvae and young juveniles of *C. limacina* are very similar to *C. antarctica* adults in having numerous oil droplets scattered throughout the integument.

Finally, the footlobes of *Clione limacina* tend to be short and wide. In comparison, all three lobes of *C. antarctica* are narrower and more elongate.

COMPARISON OF THE BUCCAL MASS

The feeding structures of *Clione* consist of three pairs of prehensile buccal cones (cephaloconi), paired hook sacs

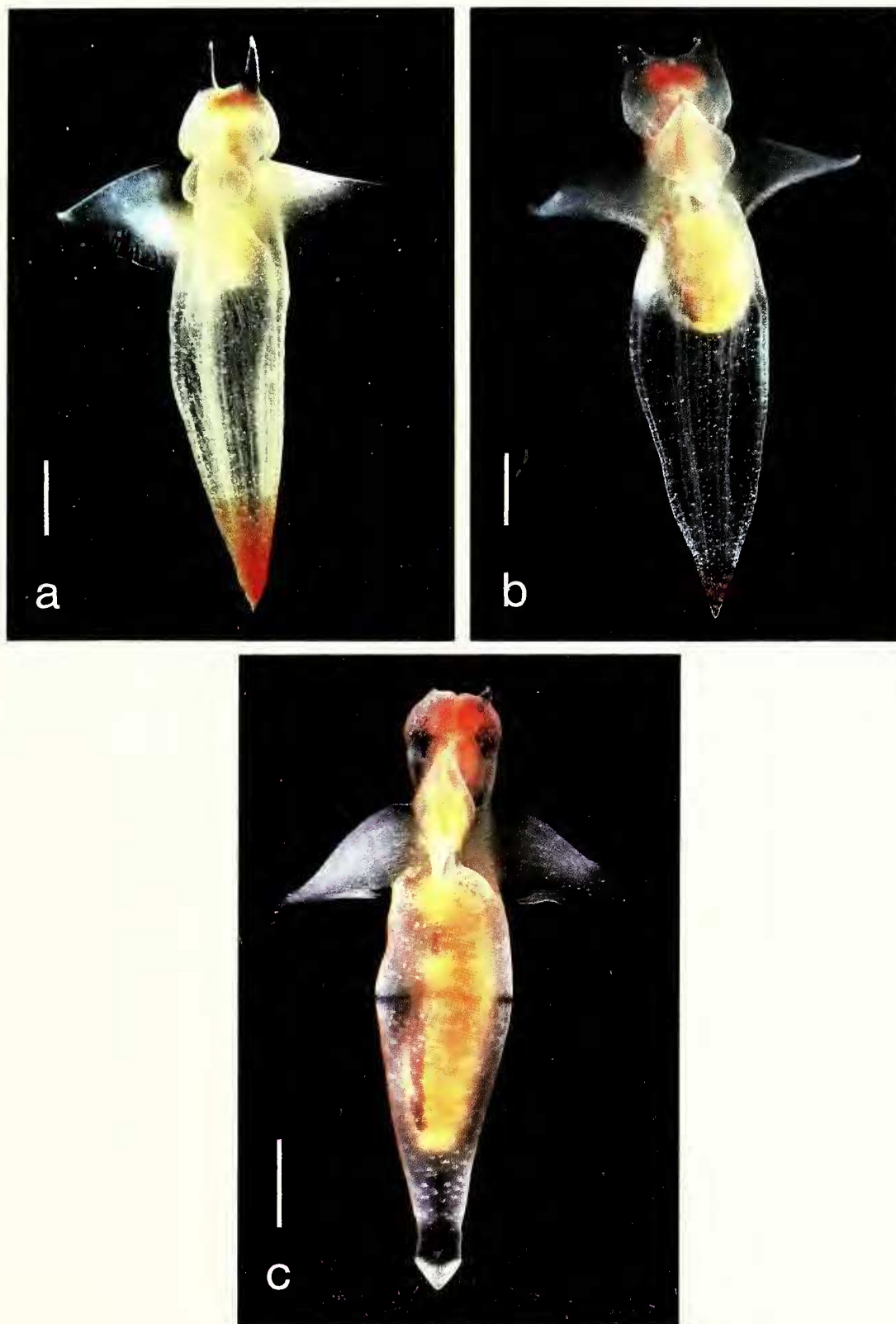


Fig. 1. Comparisons of adult *Clione* from different localities; all in ventral view: **a**, *Clione limacina* from the Subarctic Atlantic Ocean; **b**, *C. limacina* from the North Pacific Ocean; **c**, *C. antarctica* from McMurdo Sound (scale bars = 5 mm).

Table 1. A comparison of predator-prey maximal sizes in different locations.

Location	<i>Clione</i> Maximal adult length (mm)	<i>Limacina</i> Maximal adult diameter (mm)	Reference*
Subarctic Atlantic Ocean	70-85 (live)	11-12 (<i>helicina</i>)	2, 4, 8
Nova Scotia	20-25 (live)	< 3.0 (<i>helicina</i> and <i>retroversa</i>)	2
English Channel	12	ca. 1.0 (<i>retroversa</i>)	5, 6
North Pacific Ocean	< 30 (live)	2.5 (<i>helicina</i>)	1, 7, 8
Central Arctic Ocean	70-80 (live)	ca. 11 (<i>helicina</i>)	3
Antarctic Ocean	42 (live)	5-6 (<i>helicina</i>)	8

*References

- | | |
|-----------------------------|---------------------------|
| 1 - Agersborg, 1923 | 5 - Lebour, 1931 |
| 2 - Conover and Lalli, 1972 | 6 - Lebour, 1932 |
| 3 - Ospovat, pers. obs. | 7 - McGowan, 1963 |
| 4 - Lalli and Wells, 1978 | 8 - Personal observations |

containing curved chitinous hooks, and the radula. There is no obvious morphological difference between the buccal cones of *Clione limacina* and *C. antarctica*. Meisenheimer (1906) and Eliot (1907) claimed that, in *C. antarctica*, the dorsal pair of cones was spatially separated from the other two pairs and that the medial cones were the largest; in contrast, the cones were said to be equidistant in *C. limacina*, with the dorsal cones being largest. We were not able to confirm this to our satisfaction. Instead, it would appear that size and relative placement of the buccal cones is dependent on their state of eversion or contraction in living animals, or on their degree of contraction in preserved specimens.

On the other hand, differences can be found in the structure of the chitinous hooks of the two species (Fig. 2). In all *Clione*, the hook sacs contain a variable number of hooks that can be everted from the sacs. These range in size from very small to fully developed, long, curved hooks. In the largest-sized adult *Clione limacina* from Subarctic waters of the North Atlantic Ocean, each hook sac contains approximately 60 hooks; these are arranged roughly in three rows, with the largest hooks being about 1.7 mm in length (Fig. 2a). In *Clione* from the North Pacific Ocean, the numbers and maximal size of the hooks are reduced, which is related to the smaller size of the species in this area; in adults, each sac contains about 30 hooks, with the largest about 0.7 mm in length. The hooks of *C. antarctica* are more numerous and larger relative to body size than those of *C. limacina*. In adult *C. antarctica*, each sac contains approximately 60 hooks, the largest is about 1.2 mm in length (Fig. 2b).

The most striking differences between the two species occur in the morphology of the radula. The radula of *Clione limacina* (Figs. 3, 4) consists of a relatively wide ribbon that extends dorsally and ventrally over the tip of the odontophore. Each row of chitinous radular teeth consists of a single, central, sickle-shaped tooth and, in our specimens, up to 12 curved, pointed, lateral teeth on each side. The number of rows of teeth and the number of teeth in each row varies with the size of the individual examined, and these numbers are maximal in the large Subarctic Atlantic Ocean specimens (Fig. 3a). However, apart from relative numbers of teeth and relative

size differences in the teeth, there is little difference in the structure of the radula and radular teeth between North Atlantic Ocean and North Pacific Ocean *Clione* populations. In all specimens of *C. limacina* that we examined, the central tooth is well developed, even in young specimens. Denticulation of the central tooth varies from sharp points on newly formed teeth (Figs. 3c, 4b) to low, broad protuberances on older teeth (Fig. 3b), indicating wear from use. There is also no discernible difference in the general shape of the lateral teeth between populations of *C. limacina* (Figs. 3a, 4a).

In contrast, the radula of *Clione antarctica* (Fig. 5) is extremely reduced, and this reduction is not proportionate to size differences between this species and the northern *Clione*. In Antarctic *Clione*, the minute radular ribbon is positioned differently on the odontophore. The ribbon splits just anteriorly to the radular sac and then extends forward as a broadening Y-shaped structure that spreads laterally over the tip of the odontophore (Fig. 5a). The lateral radular teeth (Fig. 5b) are smaller but similar in shape to those of *C. limacina*; the number of lateral teeth in each row is somewhat variable but is less than eight in all specimens examined. The most unusual feature is the absence of a central tooth. Although Eliot (1907) illustrated median teeth which he claimed were present in the first two rows of the radula, we have not been able to confirm this and concur with Pruvot-Fol (1932) who also did not find central teeth. Because of the lateral positioning of the ribbon on the odontophore tip, the only place where such teeth could be present would be immediately anterior to the radular sac (Eliot's "hindmost" rows). Examination with scanning electron microscopy (Figs. 5c, d), revealed that the bases of adjoining lateral teeth were attached and that these eventually pull away and separate as the ribbon splits laterally. We believe that the small point of attachment of the lateral teeth in this area was seen at lower magnifications by Eliot and confused with a denticle of a central tooth.

BEHAVIORAL COMPARISONS

All *Clione* feed on the thecosomatous pteropod *Limacina* by extracting the prey from its shell. In northern cold waters, *Clione limacina* feeds on *L. helicina* (Phipps), as does

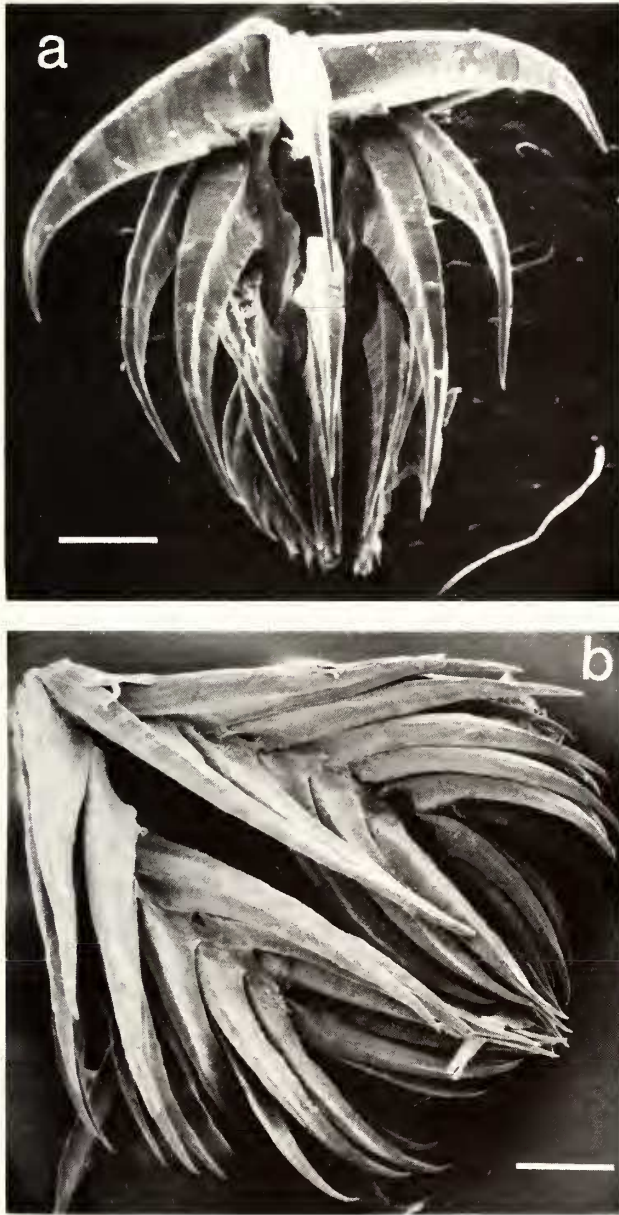


Fig. 2. Scanning electron micrographs of the hooks from a single hook sac: **a**, *Clione limacina* (North Atlantic); **b**, *C. antarctica* (scale bars = 50 μm in **a**; 200 μm in **b**).

C. antarctica in the Antarctic Ocean. In temperate waters of both the northern and southern hemispheres, *Clione* spp. co-exist with and feed on *L. retroversa* (Fleming). There are no significant differences in prey capture and feeding behavior between the two species of *Clione*. Maximal sizes attained by the predator and prey in different areas are linked (Table 1); both the prey and predator are largest in Subarctic waters and smallest in the English Channel. Antarctic Ocean species are intermediate in size. These size relationships in nature agree with the experimental laboratory results of Conover and Lalli (1972, 1974) suggesting that prey size over prey concentration and temperature is the major determinant of *Clione* size.

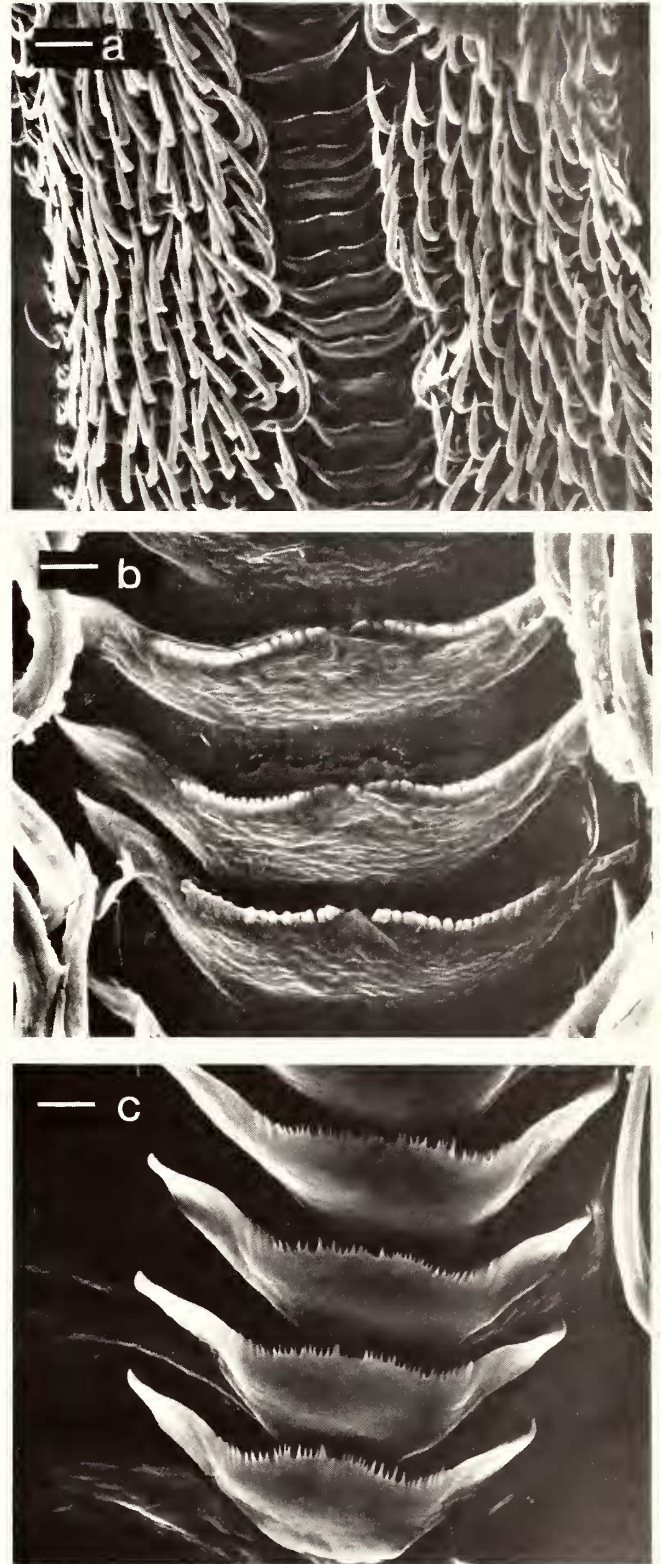


Fig. 3. Scanning electron micrographs of the radula of *Clione limacina* from the Subarctic Atlantic: **a**, median and lateral radular teeth; **b**, older median teeth showing wear; **c**, newly formed teeth (scale bars = 25 μm in **a**, 5 μm in **b** and **c**).

Swimming behavior of *Clione* has been observed *in situ* and in the laboratory. The majority of *Clione limacina* observed in the field are oriented head up and are simply maintaining their depth position with slow wing movements. During such periods of inactivity, subarctic specimens in water temperatures of less than 2°C move their wings dorsally and ventrally at a rate of about 2 beats/sec. The posterior tip of an animal is often curved ventrally at this time. When disturbed, the animals swim rapidly and the orientation of the body can be in any direction away from the disturbance. Individuals with body lengths exceeding 70 mm can swim at speeds of at least 10 cm/sec in waters of -0.5°C. The body of an animal often flexes dorsally and ventrally during rapid swimming and turning. Rapid wing motion can also be apparent during prey capture, but this does not necessarily result in movement. Slow, rhythmic swimming is continuous during mating, but rapid swimming in a circular pattern appears to be necessary to break the pairing. Spawning individuals swim slowly, moving their wings at about 2 beats/sec.

Clione limacina also appears to be able to achieve neutral buoyancy. On numerous occasions, divers have observed *C. limacina* hanging motionless in a head down position, with the wings extended. No measurable sinking occurs at such times.

In McMurdo Sound, Antarctica, *Clione antarctica* is generally found congregated near the undersurface of the ice shelf. It is generally sparsely distributed in water deeper than 20 m. Like *C. limacina*, this species also orients head up during slow rhythmic swimming, but it does not bend the posterior tip of the body ventrally. Wing motion is generally slow, at less than 2 beats/sec. When disturbed, however, large specimens (> 25 mm long) accelerate the wing beat to 4 to 5 beats/sec and can swim at speeds of about 5 cm/sec. This species reacts differently to disturbance. Most often, disturbed *C. antarctica* will stop swimming motions, retract the head slightly, and remain motionless in the water. Animals seldom attempted to swim away from a disturbance, which is the most common reaction of *C. limacina*.

Reproductive anatomy, copulation, spawning, and development are well known for *Clione limacina*, and these activities have been reviewed by Lalli and Gilmer (1989). Reproductive anatomy and behavior are not well known in the Antarctic species. Histological studies were made of four specimens of *C. antarctica* collected between November and January, when both spawning adults and veliger larvae were present. Specimens as small as 15 mm in length (preserved measurement) had oocytes in the gonad, sperm packed into a swollen genital duct, well developed mucous and albumen glands, and a large penis and prostrate gland. Two specimens of 30 to 40 mm length (live measurements) had spawned in the laboratory. Neither of these individuals showed any regression of copulatory structures and both had masses of sperm in the genital duct, indicating that they were capable of functioning as both male and female. However, copulation has never been observed in this species, either in the field or in laboratory-maintained individuals.

The size of the egg mass and the number of eggs spawned by three specimens of *Clione antarctica* varied with body size. The smallest individual (24 mm long, live measurement) produced an egg mass of 12 mm diameter containing 250 eggs. Two animals (33 mm and 38 mm long) spawned egg masses of 15 mm, with about 600 eggs produced by the smaller individual and about twice that many deposited by the larger animal. The largest egg mass was kept in the laboratory at 2°C (approximately 2.5°C above ambient temperature), and developmental times were recorded. On 12 November 1987, 24 hr after spawning, 20% of the eggs were at the second cleavage. At 400 hr, most embryos were spinning inside their egg capsules. About 10% had hatched as free-swimming veligers by approximately 20 days after spawning.

Veligers of *Clione antarctica* (Fig. 6) are characterized by a bilobed velum and a small shell with two distinctive areas. The cap-like embryonic portion of the shell measures about 110 μ m long and 160 μ m at its widest diameter. The post-embryonic extension of the shell, which is formed after

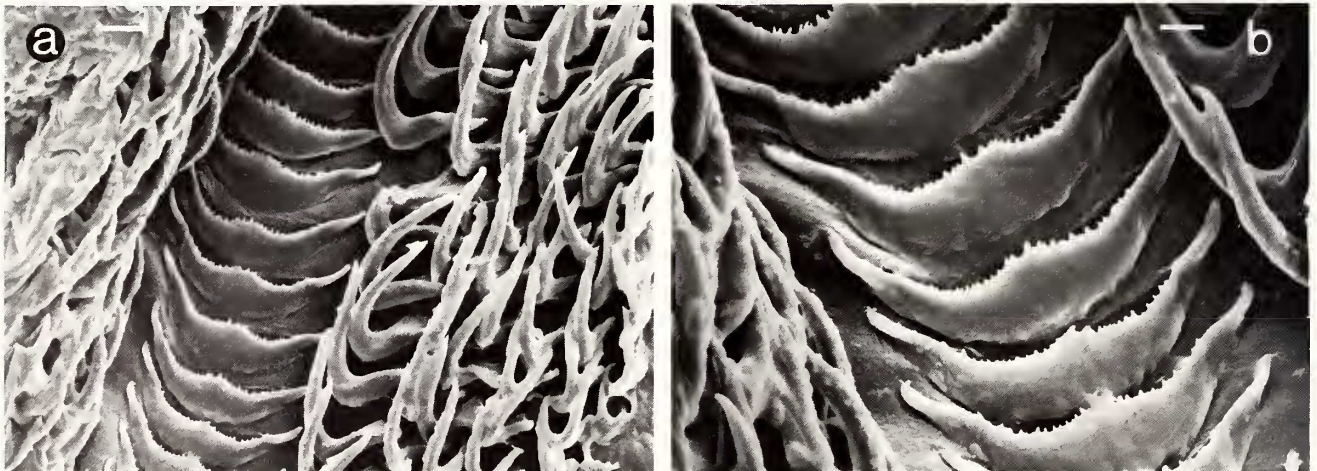


Fig. 4. Scanning electron micrographs of the radula of *Clione limacina* from the North Pacific: a, median and lateral radular teeth; b, median teeth (scale bars = 10 μ m in a, 5 μ m in b).

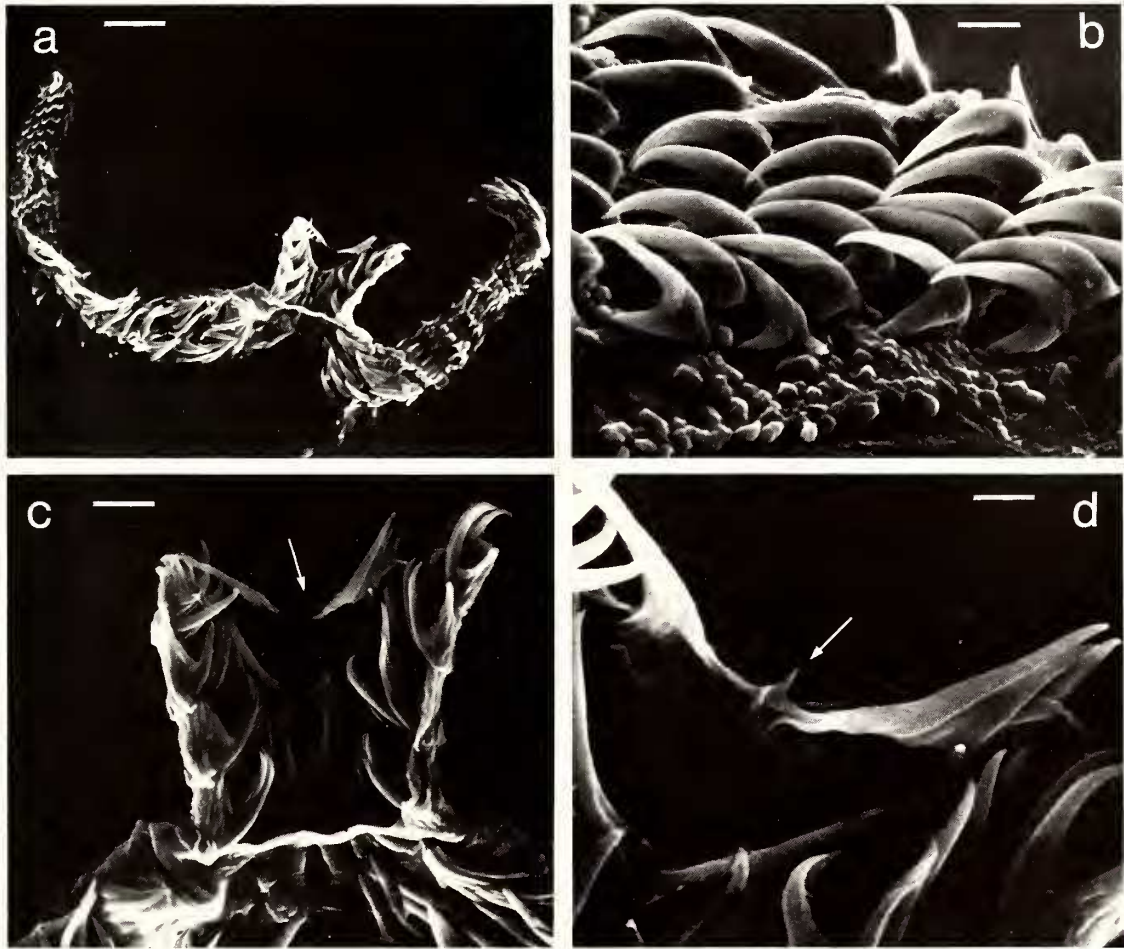


Fig. 5. Scanning electron micrographs of the radula of *Clione antarctica* from McMurdo Sound: **a**, configuration of the complete radula; **b**, lateral radular teeth; **c**, adjoined lateral teeth in the median furrow (arrow indicates fused teeth); **d**, enlargement of **c** (scale bars = 40 μm in **a**, 8 μm in **b**, 12 μm in **c**, 4 μm in **d**).

hatching, flares out like a collar from the embryonic shell and has distinctive, encircling growth rings. The shells differ from those of *C. limacina* veligers (see Lalli and Conover, 1976) in being more rounded posteriorly, with a shorter and broader embryonic portion. We have not been able to determine the size at which the larval shell is cast, nor have we observed loss of the velum and metamorphosis to the polytroch stage.

The polytrochous larvae of *Clione antarctica* are similar to those of other gymnosome species in having three ciliary bands which encircle the body, but they already show the distinctive traits that separate them from the northern *Clione*. A comparison of the polytroch larvae (each 9 mm long) of *C. antarctica* and of *C. limacina* from the North Pacific (Fig. 7) shows the striking differences in head to body proportions and in footlobe shape that are also present in the adults. It is also clear that the protuberances underlying the cilia of the anterior larval band are much more prominent in *C. antarctica* larvae. At this stage, the Antarctic polytrochs already closely resemble the adults; the only major anatomical change that will accompany growth will be the gradual regression

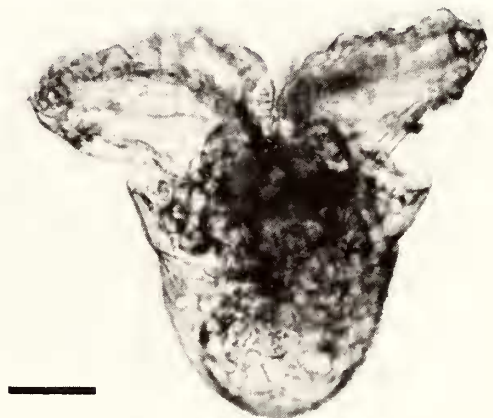


Fig. 6. Veliger larva of *Clione antarctica* (scale bar = 50 μm).

of the cilia in the larval rings. The polytrochous larvae of *C. limacina*, however, will undergo a more dramatic metamorphosis with rapid and complete loss of the anterior and middle ciliary bands, more gradual loss of the posterior ciliary ring, and a progressive lengthening of the trunk until the viscera are confined to the anterior half of the body.

DISCUSSION

Meisenheimer (1906) and Eliot (1907) were the first to present detailed accounts of *Clione* collected from the Antarctic. Both authors noted anatomical differences, but Meisenheimer preferred to regard these gymnosomes as a variety of *C. limacina*, whereas Eliot considered that the differences were such as to validate Smith's establishment of *C. antarctica*. Eliot presented a list of nine major anatomical distinctions, and several minor ones, between *C. antarctica* and *C. limacina*. We concur with many of his points concerning *C. antarctica*: the head is larger relative to body length; the body of the Antarctic species is smaller; at least two larval bands are retained into the adult stage; the viscera extend farther posteriorly; and the footlobes have a different shape and a narrower attachment. We are hesitant to accept that the buccal cones have a different arrangement, as this seems to be a preservation artifact. Nor do we agree that there are more oil droplets in the integument than there are present in *C. limacina*; this appears dependent on the size

(and age) of the animals which are compared. However, there is a tendency of Antarctic Ocean animals to develop a slight opacity of the integument compared to northern ones. On the other hand, we concur with Pruvot-Fol (1932) that Antarctic Ocean specimens do have a well-developed copulatory organ, consisting of a penis, prostrate gland and accessory organ, that is identical to that of *C. limacina*. We also share her view that median radular teeth are absent in *C. antarctica*, in contrast to the well-developed and conspicuous median teeth found even in very small specimens of *C. limacina*. In addition, our results show that the hooks of Antarctic Ocean animals are larger and more numerous relative to body size; this is probably correlated with the diminution of the radula and probably indicates a greater involvement of the hooks in extraction of prey from its shell.

Behavioral differences between the two species do not appear to be so pronounced, but this could be due to fewer hours of observation of living *Clione antarctica*. Both *C. limacina* and *C. antarctica* feed on *Limacina helicina* or *L. retroversa*; we have not observed any significant difference in prey capture or in ingestion time from that described by Lalli (1970) and Conover and Lalli (1972). The Antarctic Ocean species, however, swims at slower rates than does its northern counterpart, and it usually responds to disturbance by cessation of swimming rather than active movement away from a stimulus. Both clionids deposit free-floating, gelatinous egg masses. The size of egg masses and the number of eggs per mass are smaller in *C. antarctica* than in large, subarctic *C. limacina*, but are larger than in dwarf specimens of *C. limacina* from the English Channel (Lalli and Gilmer, 1989). In the northern species, hatching of the veligers coincides with periods of maximal phytoplankton abundance and with simultaneous hatching of *Limacina* veligers (Mileikovsky, 1970; Conover and Lalli, 1972). In the Antarctic Ocean, we have collected spawning adults from November through January, and Massy (1932) reported finding larvae of less than 3 mm length in October, November, December and February. There are differences in the size and shape of the veliger shell of *C. antarctica*, as well as between the polytroch larvae of the northern and southern species. It is interesting that *C. antarctica*, like several other gymnosome species (Lalli and Gilmer, 1989), displays neotenous characters, retaining external larval features and a relatively small size after reaching sexual maturity. In contrast, *C. limacina* usually undergoes a complete metamorphosis from the polytroch stage; a posterior larval band is present only in the small-sized individuals living in the English Channel (Lebour, 1931; Morton, 1958) or in the rare neotenous individual collected off Nova Scotia (Lalli and Conover, 1973).

Although we do not agree on all the points of difference between northern and southern *Clione* as established by earlier workers, we do believe that the evidence presented here further strengthens the taxonomic distinctions separating *C. limacina* and *C. antarctica*. Although both clionids occupy identical ecological niches in cold water areas, feeding on two species of the shelled pteropod *Limacina* and exhibiting similar behavioral patterns, they are sufficiently different morphologically to justify their separation. In addition, the

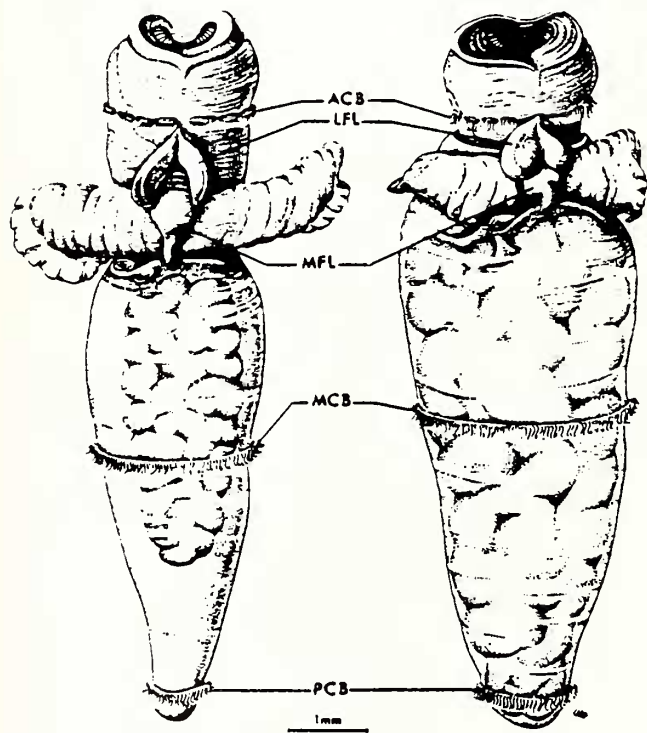


Fig. 7. Polytrochous larvae of *Clione antarctica* from the Antarctic Ocean (left) and of *C. limacina* from the North Pacific (right) (ACB, anterior ciliary band; LFL, lateral footlobe; MCB, median ciliary band; MFL, median footlobe; PCB, posterior ciliary band).

species are spatially isolated. There is no evidence to suggest that there is any physical connection between the northern and southern populations, so there is no possibility of interbreeding. However, it is evident from the similarity of the species in the two hemispheres that they have evolved from a common ancestor.

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LITERATURE CITED

- Agersborg, H. P. K. 1923. Gymnosomatous Pteropoda from Friday Harbor, Washington. *Annals of Natural Science, Zoology, Series 10* 6:391-402.
- Conover, R. J. and C. M. Lalli. 1972. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. *Journal of Experimental Marine Biology and Ecology* 9:279-302.
- Conover, R. J. and C. M. Lalli. 1974. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. II. Assimilation, metabolism, and growth efficiency. *Journal of Experimental Marine Biology and Ecology* 16:131-154.
- Ekman, S. 1953. *Zoogeography of the Sea*. Sidgwick & Jackson, London. 417 pp.
- Eliot, C. 1907. Mollusca. VI. Pteropoda. *National Antarctic Expedition 1901-1904 (Natural History)* 3 (Zoology and Botany): 1-15. British Museum, London.
- Humason, G. L. 1962. *Animal Tissue Techniques*. W. H. Freeman, San Francisco. 641 pp.
- Lalli, C. M. 1970. Structure and function of the buccal apparatus of *Clione limacina* (Phipps) with a review of feeding in gymnosomatous pteropods. *Journal of Experimental Marine Biology and Ecology* 4:101-118.
- Lalli, C. M. and R. J. Conover. 1973. Reproduction and development of *Paedoclione doliiformis*, and a comparison with *Clione limacina* (Opisthobranchia: Gymnosomata). *Marine Biology* 19:13-22.
- Lalli, C. M. and R. J. Conover. 1976. Microstructure of the veliger shells of gymnosomatous pteropods (Gastropoda: Opisthobranchia). *Veliger* 18:237-240.
- Lalli, C. M. and R. W. Gilmer. 1989. *Pelagic Snails: The Biology of Holoplanktonic Gastropod Mollusks*. Stanford University Press, Stanford, California. 259 pp.
- Lalli, C. M. and F. E. Wells. 1978. Reproduction in the genus *Limacina* (Opisthobranchia: Thecosomata). *Journal of Zoology, Proceedings of the Zoological Society of London* 186:95-108.
- Lebour, M. V. 1931. *Clione limacina* in Plymouth waters. *Journal of the Marine Biological Association of the United Kingdom* 17:785-795.
- Lebour, M. V. 1932. *Limacina retroversa* in Plymouth waters. *Journal of the Marine Biological Association of the United Kingdom* 18:123-129.
- Martens, F. 1675. *Spitzbergische oder grölandische Reise Beschreibung gethan im Jahr 1671*. Schultzen, Hamburg.
- Massy, A. L. 1920. Mollusca. III. Eupteropoda (Pteropoda Thecosomata) and Pterota (Pteropoda Gymnosomata). *British Antarctic ("Terra Nova") Expedition 1910, Natural History Report, Zoology* 2:203-228.
- Massy, A. L. 1932. Mollusca: Gastropoda Thecosomata and Gymnosomata. *"Discovery" Reports* 3:267-296.
- McGowan, J. A. 1963. Geographical variation in *Limacina helicina* in the North Pacific. In: *Speciation in the Sea*. J. P. Harding and N. Tebbel, eds. pp. 109-128. Systematics Association Publication No. 5.
- Meisenheimer, J. 1906. Die Pteropoden der deutschen Südpolar-Expedition 1901-1903. *Deutsche Südpolar-Expedition IX. Zoologie*. 1:94-153.
- Mileikovsky, S. A. 1970. Breeding and larval distribution of the pteropod *Clione limacina* in the North Atlantic, Subarctic and North Pacific Oceans. *Marine Biology* 6:317-334.
- Morton, J. E. 1958. Observations on the gymnosomatous pteropod *Clione limacina* (Phipps). *Journal of the Marine Biological Association of the United Kingdom* 37:287-297.
- Phipps, C. J. 1774. *A Voyage Towards the North Pole*. Bowyer & Nichols, London. 275 pp.
- Pruvot-Fol, A. 1932. Notes sur quelques gymnosomes de provenances diverses et diagnose d'un genre nouveau. *Archives de Zoologie expérimentale et générale* 74:507-529.
- Rang, P. C. A. L. and L. F. A. Souleyet. 1852. *Histoire naturelle des Mollusques Pteropodes. Monographie comprenant la description de toutes les especes de ce groupe de Mollusques*. J.-B. Baillié, Paris. 86 pp.
- Smith, E. A. 1902. Mollusca. In: *Report on the Collections of Natural History of the "Southern Cross"*. W. Clowes & Sons, Ltd., London. 344 pp.
- van der Spoel, S. 1976. *Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda)*. Bohn, Scheltema, & Holkema, Utrecht. 484 pp.

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